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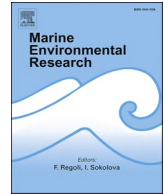
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Fucus vesiculosus populations on artificial structures have potentially reduced fecundity and are dislodged at greater rates than on natural shores

Veronica Farrugia Drakard^{a,*}, Paul Brooks^a, Tasman P. Crowe^a, Hannah S. Earp^b, Bryan Thompson^a, Nathan Bourke^a, Ruby George^b, Chloe Piper^b, Pippa J. Moore^{b,c}

^a UCD Earth Institute and School of Biology and Environmental Science, Science Centre West, University College Dublin, Belfield, Dublin 4, Ireland

^b Institute of Biological, Environmental & Rural Sciences (IBERS), Aberystwyth University, Aberystwyth, SY23 3DA, UK

^c School of Natural and Environmental Sciences, Newcastle University, Newcastle-Upon-Tyne, NE1 7RU, UK

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ABSTRACT

Artificial structures are widespread features of coastal marine environments. These structures, however, are poor surrogates of natural rocky shores, meaning they generally support depauperate assemblages with reduced population sizes. Little is known about sub-lethal effects of such structures, for example, in terms of demographic properties and reproductive potential that may affect the dynamics and long-term viability of populations. Such understanding is particularly important for ecosystem engineer species, such as the intertidal seaweed *Fucus vesiculosus*. In this study, *F. vesiculosus* was sampled on eight artificial structures and eight natural shores along the east coast of Ireland and the west coast of Wales. Algal percentage cover, biomass, density of individuals, and growth rate did not differ between artificial and natural shores. Growth and reproductive cycles were consistent with previous studies for this species. While there was considerable variation from site to site, on average, populations on natural shores produced a higher number of mature receptacles during the peak reproductive period in April, and lower rates of dislodgement than on artificial structures. As *F. vesiculosus* reach peak reproductive output after 24 months, this suggests that individuals may be removed from populations on artificial structures before reaching their full reproductive potential. In this case, this did not influence density, percentage cover, or biomass, which suggests that *F. vesiculosus* populations on artificial structures may function similarly to those on natural shores if supported by suitable source populations, but potentially may not persist otherwise.

1. Introduction

Artificial structures are increasingly widespread features of coastal marine environments with 50% of the Italian coastline on the northern Adriatic Sea armoured, 46% of English coastlines protected by artificial structures, and 50% of Sydney Harbour in Australia consisting of seawalls (Firth et al., 2013). Many of these structures – including seawalls and breakwaters – are installed for the purposes of coastal defence, and therefore it is likely that they will proliferate further as global sea levels continue to rise and the frequency of intense storms increases (Firth et al., 2014a; Mayer-Pinto et al., 2019).

Coastal defence structures and other artificial substrata constitute new hard substrata in the marine environment, and may therefore themselves be colonised by marine species (Naylor et al., 2012). However, the habitat they provide differs from that of a natural shoreline in a

variety of ways. In particular, artificial structures tend to be constructed of different materials, including concrete, and have lower surface heterogeneity with fewer microhabitats available for colonisation (Green et al., 2012; Firth et al., 2014b). Furthermore, there may be differences between types of artificial structures in terms of habitat structure and topography. In particular, the complexity and heterogeneity of microhabitats provided by rip-rap structures such as breakwaters is generally greater than that provided by seawalls (Bulleri and Chapman, 2004). Consequently, artificial structures present very different challenges for potential colonisers, and a growing body of research indicates that the resultant biotic assemblages tend to be relatively impoverished when compared to those established on natural rocky shores (Chapman and Bulleri, 2003; Bulleri and Chapman, 2004; Bulleri, 2005a). This suggests that as coastal urbanisation expands, natural coastlines, in particular areas of soft sediment, are being replaced by surfaces that are not

* Corresponding author.

E-mail address: veronica.farrugidrakard@ucdconnect.ie (V.F. Drakard).

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equivalent in their ability to support biological assemblages and provide ecosystem services (Aguilera, 2018).

As a function of the differences between natural rocky reefs and artificial structures there has been significant interest in the concept of ecological engineering, or eco-engineering, which aims to combine ecological knowledge and engineering criteria to modify artificial substrata in such a way as to allow them to support biological assemblages that more closely approximate a natural state in terms of both structure and function (Browne and Chapman, 2011). A number of eco-engineering strategies have been explored in the context of marine environments, including the identification of alternative materials for construction (Dennis et al., 2018), modification of surface textures (Coombes et al., 2015), and the addition of microhabitats, in particular water-retaining features (Browne and Chapman, 2014; Evans et al., 2015; Firth et al., 2016; Morris et al., 2017). To develop eco-engineering solutions that provide the greatest overall benefit, it is necessary to identify specific differences in biological assemblages between artificial and natural structures. Subsequently, it is necessary to identify which aspects of these assemblages can be successfully modified on artificial surfaces. Thus far, most studies have focused on broad ecological concepts such as assemblage structure, species composition, and relative abundances (Chapman and Bulleri, 2003; Bulleri et al., 2005; Brook et al., 2018). In contrast, few studies have compared the ecological success of individual taxa on artificial and natural surfaces (Moreira et al., 2006; Fauvelot et al., 2009; Cacabelos et al., 2016; Morris et al., 2017). Influences of artificial structures on population structure, demographic properties and reproductive potential could affect the long-term viability and productivity of populations.

Additionally, there has been only limited investigation into how seaweed population structure and function differs between artificial and natural substrata in the marine environment (Bulleri, 2005b; Airolidi and Bulleri, 2011; Ferrario et al., 2016; Mayer-Pinto et al., 2018). Macroalgae are fundamental to both the trophic and physical structure of marine shallow-water ecosystems (Hurd et al., 2014). As primary producers, they are a source of nutrients for organisms at higher trophic levels and underpin trophic exchanges both in-situ and ex-situ via spatial subsidies (Vadas and Steneck, 1988; Piñeiro-Corbeira et al., 2018). Furthermore, they provide shelter for a variety of juveniles and prey species and may themselves act as a substratum for a suite of epiphytic flora and fauna (Christie et al., 2009). Many of the larger phaeophyte species, in particular members of the Orders Laminariales and Fucales, are considered to be ecosystem engineers (Dayton, 1985; Vadas et al., 2004a; Teagle et al., 2017). This is defined as an organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials (Jones et al., 1994). Coastal urbanisation therefore has the potential to influence ecosystem function through effects on such species (Mayer-Pinto et al., 2018; Mayer-Pinto et al., in press).

One such ecosystem engineer is *Fucus vesiculosus* L., a phaeophyte within the Order Fucales. This species is common in the intertidal zone of coastal areas of the North Atlantic where its highly-branched canopy structure creates a unique habitat (Rinne and Salovius-Laurén, 2020). It is a dioecious species, which shows initiation of receptacle development in mid-winter with maximum fertility in early summer (Knight and Parke, 1950; Billard et al., 2005). Additionally, a number of studies have characterised the seasonal growth patterns and colonisation dynamics of this species, consisting of slow growth during winter and early spring followed by rapid growth throughout summer and autumn (Knight and Parke, 1950; Keser and Larson, 1984). Consequently, *F. vesiculosus* is an ideal focal species to investigate differences in the population structure, demographic properties and reproductive potential of habitat-forming intertidal seaweeds between artificial and natural shores.

In general, artificial structures tend to be subject to high levels of both natural and anthropogenic disturbance, and may therefore potentially present a more stressful environment for habitat-forming intertidal seaweeds (Airolidi and Bulleri, 2011). This is related to the fact that

many of these structures are constructed for the purposes of coastal defence against erosion and flooding, and as such are themselves subjected to increased sediment scour and disturbance as a result of storms (Moschella et al., 2005; Airolidi and Bulleri, 2011). Seaweed populations subjected to such high levels of disturbance may allocate more resources towards vegetative growth than reproductive development, which would have an impact on the fecundity and sustainability of these populations (Ruuskanen and Bäck, 1999; Rothäusler et al., 2018).

The aim of this study was to characterise and compare populations of a key habitat-forming species on natural and artificial substrata in terms of their population structure. The following hypotheses were tested:

- (1) The percentage cover, density, and biomass of *F. vesiculosus* are reduced on artificial structures compared to natural shores.
- (2) Growth of *Fucus vesiculosus* is reduced on artificial structures compared to natural shores.
- (3) *F. vesiculosus* individuals are more likely to be dislodged from artificial structures compared to natural shores.
- (4) The number of reproductive apices produced by *F. vesiculosus* is reduced, and reproductive cycle and sex ratios are altered on artificial structures compared to natural shores.

These were tested by sampling natural shores in both Ireland and Wales in order to enable an assessment of the generality of the patterns observed.

2. Methodology

2.1. Experimental design

Sixteen sites along the east coast of Ireland and the west coast of Wales were selected for this study, consisting of eight artificial structures and eight natural shores (Fig. 1). Of the artificial structures, six were rip-rap structures and two were seawalls. The artificial structures were composed of granite boulders in the case of the rip-rap structures and concrete in the case of the two seawalls. The natural shores were composed of mudstones in Wales, and limestone or granite in Ireland, and varied in topographic complexity. Both natural and artificial structures were similar in environmental context, being fully marine and moderately exposed to wave action. All experiments were conducted within the zone of peak occurrence of *Fucus vesiculosus* between the mean tide level (MTL) and mean high water neaps (MHWN) of each site.

2.2. Field protocols

2.2.1. Cover, density, and biomass of populations

Measures of percentage cover and density of *F. vesiculosus* were undertaken in December 2018. Ten 0.25 m² quadrats were haphazardly deployed at each site on horizontal to gently sloping surfaces. These quadrats were each subdivided into 25 sub-quadrats, and percentage cover within each sub-quadrat was estimated between 0% and 4% using a methodology based on Dethier et al. (1993). The estimates for each sub-quadrat were then added up to give an estimate of the total percentage cover of *F. vesiculosus* canopy within each quadrat. The number of holdfasts was counted and taken as a measure of the number of individuals per quadrat. In each quadrat two individuals were randomly removed and their wet weight biomass was determined *in situ* using a digital balance. For the eight sites located along the coast of Wales, biomass measurements were repeated in April and July 2019.

2.2.2. Length and growth of individuals

In November 2018, three patches of 1 × 1 m were marked out at each site on horizontal to gently sloping surfaces, and five individuals were randomly selected to be measured and tagged within each patch. The total length of each individual was measured from the holdfast to the apex of the longest frond. Individuals were then tagged and growth rates

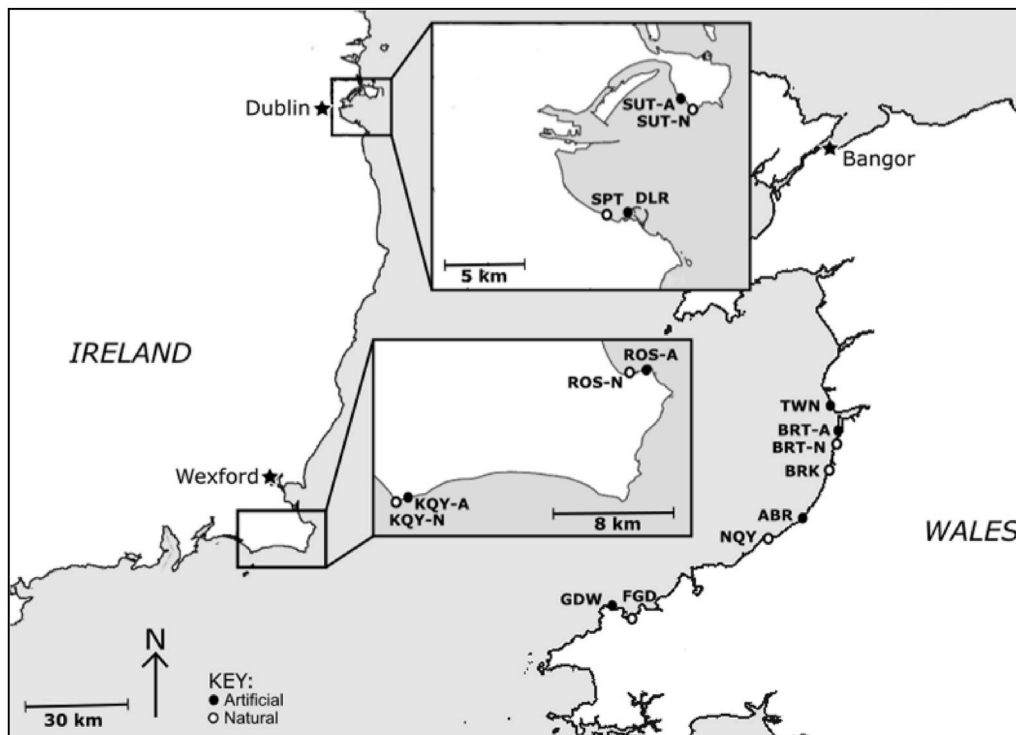


Fig. 1. Map of the Irish Sea showing artificial structures (black circles) and natural sites (white circles) selected for sampling. ROS – Rosslare Harbour (artificial (A) and natural (N)), KQY – Kilmore Quay (A and N), SUT – Sutton (A and N), SPT – Seapoint (N), DLR – Dun Laoghaire (A), TWN – Tywyn (A), BRT – Borth (A and N), BRK – Bath Rocks (N), ABR – Aberaeron (A), NQY – New Quay (N), FGD – Fishguard (N), GDW – Goodwick (A).

were monitored using an adaptation of the hole-punch method (Parke, 1948; Vadas et al., 2004b). At Irish sites, five healthy apical tips were selected per individual and a 3 mm diameter hole was punched 2 cm below each apex. At each subsequent sampling point, the distance from each punched hole to its respective apical tip was measured and the increment of growth for each individual was calculated. Sampling was conducted in January, April, and August 2019 to encompass potential periods of peak and minimal growth (Keser and Larson, 1984; Carlson, 1991). At Welsh sites, three healthy apical tips were selected per individual and a 3 mm diameter hole was punched 2 cm below each apex. After six weeks, the distance from each punched hole to its respective apical tip was measured and the increment of growth for each individual was calculated. The hole-punch method was then repeated in April, June, and July 2019 and in each case, growth for each individual was measured six weeks later. Growth was presented as apical extension (mm) per week, therefore total growth was divided by the number of weeks between growth measurements.

2.2.3. Dislodgement

In November 2018, three patches of 2×0.5 m were identified at each site on horizontal to gently sloping surfaces. Within each patch, 10 individuals were randomly selected and tagged for the purposes of monitoring the overall rate of dislodgement. At each subsequent sampling point in January, April, and August 2019, the number of tagged individuals remaining was recorded. Rate of dislodgement for winter, spring, and summer was calculated as the number of individuals dislodged as a proportion of the total number of individuals present at the start of each season.

2.2.4. Production of receptacles, receptacle maturity, and sex

Sampling was undertaken at reproductive onset (November 2018), prior to peak reproduction (April 2019), during peak reproduction (June 2019) and after peak reproduction (August 2019), as indicated by the literature (Bäck et al., 1993). Ten 50×50 cm quadrats were deployed

haphazardly on horizontal to gently sloping surfaces between the mid-tide line (MTL) and the mean high water neaps (MHWN) of each site. Thirty individuals were randomly collected from each site and taken back to the laboratory to determine reproductive effort and sex ratios.

For each individual, a single mature frond of length >30 cm was selected, and the total number of apices (incision of dichotomy >0.5 cm) and number of reproductive apices were counted. These measures were used to calculate a fecundity index (F.I.), calculated as the number of fertile apices (i.e. receptacles) per individual as a proportion of the total number of apices per individual (Ruuskanen and Bäck, 1999). The stage of maturity of a maximum of 30 reproductive apices was then identified according to the system described in Table 1. If individuals were classed as stage 2 or above, three receptacles were removed for the purposes of identifying the individual as male or female.

Table 1

Stages of receptacle formation in *Fucus vesiculosus*, adapted from (Knight and Parke, 1950).

| Stage | Description |
|-------|--|
| 1 | A slight swelling at the tips felt using fingertips or the naked eye. Sometimes a change in colouration (paler/creamy colour) and conceptacles visible at the very tips. |
| 2 | Longer receptacle with conceptacles clear but pale |
| 3 | Conceptacles darker than stage 2, and the receptacle is inflated. |
| 4 | Receptacle is as per stage 3 but is noticeably deflated |
| 5 | Receptacles are degrading. |
| 6 | Only the base of the receptacle is still evident (0.2–0.5 cm) with evidence of degrading or/and emptied conceptacles in receptacle base. |
| 7 | The majority or the entire receptacle has senesced (≤ 0.1 mm of the receptacle remaining) and is not evident at the tip of the frond. Often only the degrading lamina or bare midrib is remaining. |

2.3. Data analysis

All statistical analyses were carried out on untransformed data using PRIMER v7 (Clarke and Gorley, 2015) with PERMANOVA+ (Anderson et al., 2008) or RStudio (2019). For analyses performed using PERMANOVA similarity matrices were based on Euclidean distances and 9999 permutations were performed on residuals under a reduced model. PERMDISP analyses were performed to test for homogeneity of dispersions and *post-hoc* pairwise PERMANOVAs were applied to explore significant effects. When the assumption of homogeneity of dispersions was not satisfied, factors were investigated at a significance level of $p = 0.01$.

Percentage cover, density, and biomass of *F. vesiculosus* populations were analysed using three-way PERMANOVAs with Type (Artificial or Natural), Coast (Ireland or Wales), and Site (nested in Type and Coast) as factors. Growth per week (mm) of *F. vesiculosus* individuals was analysed using three-way PERMANOVAs with Month, Type, and Site (nested in Type) as factors. The Welsh and Irish datasets were analysed separately due to differences in methods of data collection for growth. The proportion of *F. vesiculosus* individuals dislodged was analysed by four-way PERMANOVA with Type, Season, Coast, and Site (nested in Type and Coast) as factors.

The total number of receptacles and the fecundity index were analysed with four-way PERMANOVAs with Month, Type, Coast, and Site (nested in Type and Coast) as factors. Sex ratios were analysed by building a binomial generalized linear model (GLM) with sites as replicates and carrying out an Analysis of Deviance with Type III sum of squares to generate likelihood ratio results. *Post-hoc* Tukey adjusted comparisons were generated using the 'lsmeans' function of the 'emmeans' package (Lenth, 2020) when significant effects were detected. To investigate associations between receptacle maturity and the factors Coast, Month, and Type, Chi-squared (X^2) tests were applied and graphs of relevant associations for these tests were produced.

3. Results

3.1. Gaps in the data

The loss of *F. vesiculosus* individuals or other circumstances beyond the authors' control led to a number of gaps in the dataset. First of all, cover, density and biomass data were collected from only six sites in Wales rather than eight: three artificial structures and three natural shores. Secondly, growth data were collected only during December and April in Ireland, as loss of individuals precluded collection of data during the summer season. Thirdly, growth and dislodgement data were collected from seven sites in Ireland and eight sites in Wales. Finally, reproduction data were collected from seven sites in Ireland and eight sites in Wales up to April. From June onwards, data were collected from all sixteen sites.

3.2. Cover, density, and biomass of populations

Percentage cover and biomass did not differ between artificial (mean % cover = $59.79 \pm 5.41\%$; mean biomass = 51.22 ± 20.86 g) and natural shores (mean % cover = $64.27 \pm 5.77\%$; mean biomass = 63.43 ± 17.05 g) (Table 2). There was, however, significant variation among sites (nested in shore type and coast) suggesting small scale variability in population structure (Table 2).

Although the density of *F. vesiculosus* appeared to be greater on artificial structures than on natural shores in Wales (Fig. 2), this pattern was not statistically significant (Table 2). Similarly, there was no significant difference in density of individuals between artificial and natural shores in Ireland (pairwise PERMANOVA Ireland Art v Ireland Nat $t = 0.04$, $p = 1$). However, density of individuals was significantly greater on artificial shores in Wales than on artificial shores in Ireland (pairwise PERMANOVA Ireland Art v Wales Art $t = 5.20$, $p < 0.05$).

Table 2

Permutational ANOVAs for percentage cover, density, and biomass of *F. vesiculosus* between natural rocky reefs and artificial structures along Irish Sea coastlines. Similarity matrix is based on Euclidean distance of untransformed data. Bold text indicates significant values. Significance was accepted at $p < 0.05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < 0.01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

| Source of variation | df | Percentage cover | | Density | | Biomass | |
|---------------------|-----|------------------|---------------|---------|---------------|---------|---------------|
| | | F | p | F | p | F | p |
| Coast = C | 1 | 7.14 | 0.03 | 9.60 | <u>0.02</u> | 0.02 | 0.88 |
| Shore Type = T | 1 | 0.47 | 0.52 | 9.08 | 0.01 | 0.19 | 0.65 |
| Site (C x T) | 10 | 4.76 | 0.0001 | 4.02 | 0.0002 | 6.74 | 0.0001 |
| C x T | 1 | 0.00 | 0.97 | 8.75 | 0.01 | 1.09 | 0.39 |
| Res | 126 | | | | | | |
| Total | 139 | | | | | | |

3.3. Lengths of individuals and rate of growth

Mean total length did not differ between artificial (mean length 33.63 ± 4.71 cm) and natural (mean length 37.76 ± 3.32 cm) shores (Table 3). There was, however, significant variability between sites nested within shore type (Table 3) and a significant difference between lengths measured in Ireland (mean length 27.93 ± 2.44 cm) and Wales (mean length 42.75 ± 3.22 cm) (Table 3).

In Wales, growth was highly variable between sites nested in shore type, but there was no difference in growth rates between artificial and natural shores (Table 4). While variable across sites, growth rates in June and July were generally greater than those in December and April (Fig. 3A). Growth rates in Ireland were highly variable between sites nested in shore type, but were also found not to be significantly different between artificial and natural shores or among months (Fig. 3B).

3.4. Rate of dislodgement

Dislodgement was highly variable between sites nested within shore type and coast, and there was a significant difference in dispersion of samples between sites ($F_{14, 120} = 6.85$, $p < 0.05$). In particular, the artificial site KQY-A showed the highest dislodgement in April and June, while DLR and BRT-A showed very high dislodgement in August. In terms of natural sites, KQY-N and ROS-N consistently had the highest rates of dislodgement. Overall, however, the analysis revealed that there was on average a higher rate of dislodgement on artificial structures compared to natural shores (Fig. 4, Table 5). This is particularly clear when comparing Irish artificial structures to Irish natural shores, and Welsh artificial structures to Welsh natural shores within a given month (Fig. 4). There was variation in the way the sites within a shore type differed from each other from month to month (Table 5). However, pairwise comparisons for levels of Site(Coast x Type) within each month and for levels of Month within each site were unable to discern where those differences lay. A significant difference was also observed between rates of dislodgement in Ireland and Wales; in general, dislodgement was higher at Irish sites across all months, but this did not vary between shore types (Fig. 4, Table 5).

3.5. Production of receptacles, receptacle maturity and sex

3.5.1. Fecundity index

A peak in the fecundity index on both natural and artificial shores was observed between late spring and early summer, with a peak in April on natural shores and in June on artificial structures (Fig. 5). There was variation in the way the sites within a shore type differed from each other from month to month, and *post-hoc* pairwise comparisons suggested significant differences both for levels of Site(Coast x Type) within

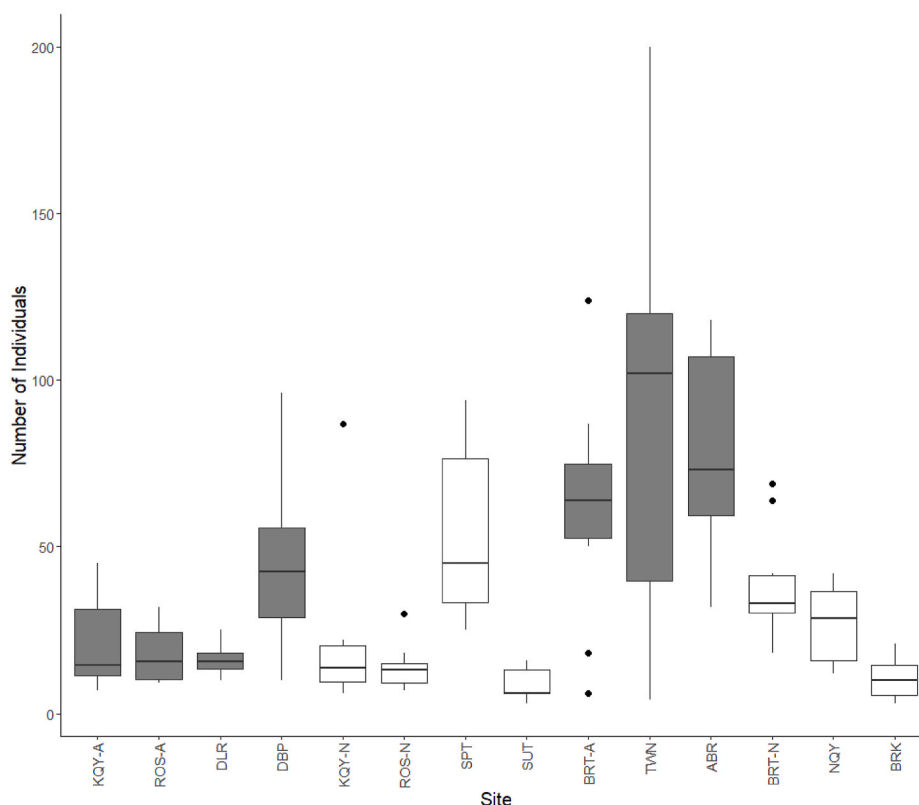


Fig. 2. Densities of *F. vesiculosus* per 0.25 m² at each site. Artificial sites in grey, natural sites in white. Sites KQY-A to SUT are in Ireland, while sites BRT-A to BRK are in Wales.

Table 3

Permutational ANOVAs for lengths of *F. vesiculosus* populations between natural rocky reefs and artificial structures along Irish Sea coastlines. Similarity matrix is based on Euclidean distance of untransformed data. Bold text indicates significant values. Significance was accepted at $p < 0.05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < 0.01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

| Source of variation | df | F | P |
|---------------------|-----|-------|---------------|
| Coast = C | 1 | 15.06 | 0.004 |
| Shore Type = T | 1 | 1.86 | 0.20 |
| Site (T) = S(T) | 11 | 6.96 | 0.0001 |
| C x T | 1 | 0.30 | 0.60 |
| Res | 309 | | |
| Total | 323 | | |

each month and for levels of Month within each site (Table 6). The fecundity index was significantly higher on natural shores (mean = 0.78 ± 0.03) compared to artificial structures (mean = 0.65 ± 0.05) in April (Fig. 5; Table 6), but for all other months there was no difference between shore types. This difference in fecundity index during April is relatively more pronounced in Ireland (mean NAT = 0.74 ± 0.04 , mean ART 0.54 ± 0.04) than in Wales (mean NAT = 0.81 ± 0.04 , mean ART = 0.72 ± 0.06).

The fecundity index on artificial structures was higher in April than in December and lower in July/August than in June (Fig. 5; Table 6). However, there was no difference in the fecundity index between April and June (Table 6). On natural shores, fecundity index for each month was found to be significantly different to that of the subsequent month (Table 6). There was also a significant effect of Coast on the fecundity index (Fig. 5; Table 6), with higher values in Wales than in Ireland across all months.

Table 4

Permutational ANOVAs for growth of *F. vesiculosus* populations between natural rocky reefs and artificial structures along Irish Sea coastlines. Similarity matrix is based on Euclidean distance of untransformed data. Bold text indicates significant values. Significance was accepted at $p < 0.05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < 0.01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

| Source of variation | Wales | | | Ireland | | |
|---------------------|-------|-------|---------------|---------|------|-------------|
| | df | F | p | df | F | p |
| Month = M | 3 | 26.36 | 0.0001 | 1 | 0.01 | 0.91 |
| Shore Type = T | 2 | 0.72 | 0.69 | 1 | 0.33 | 0.41 |
| Site (Type) = S(T) | 7 | 5.00 | 0.007 | 4 | 3.34 | 0.01 |
| M x T | 3 | 0.05 | 0.98 | 1 | 4.57 | 0.13 |
| M x S(T) | 16 | 2.91 | 0.008 | 3 | 0.44 | 0.72 |
| Res | 848 | | | 72 | | |
| Total | 879 | | | 82 | | |

3.5.2. Sex of individuals and receptacle maturity

In terms of sex ratio, the interaction between shore type and coast was found to be significant (Table 7); *post-hoc* pairwise comparisons suggested a significant difference between Ireland and Wales within shore type 'Natural', and between artificial and natural shores within each coast. Male individuals were found in higher proportions on Welsh natural shores while females were found in higher proportions on Irish natural shores (Fig. 6). Furthermore, in general there was a greater proportion of females on artificial structures than on natural shores on both coasts. There was also a significant association between month and sex ratio (Table 7), with the relative proportion of females increasing as the reproductive season progressed towards July/August (Fig. 7).

In terms of receptacle maturity, there was a significant association between maturity stage and shore type ($X^2 = 187.48$, $p < 0.05$). A

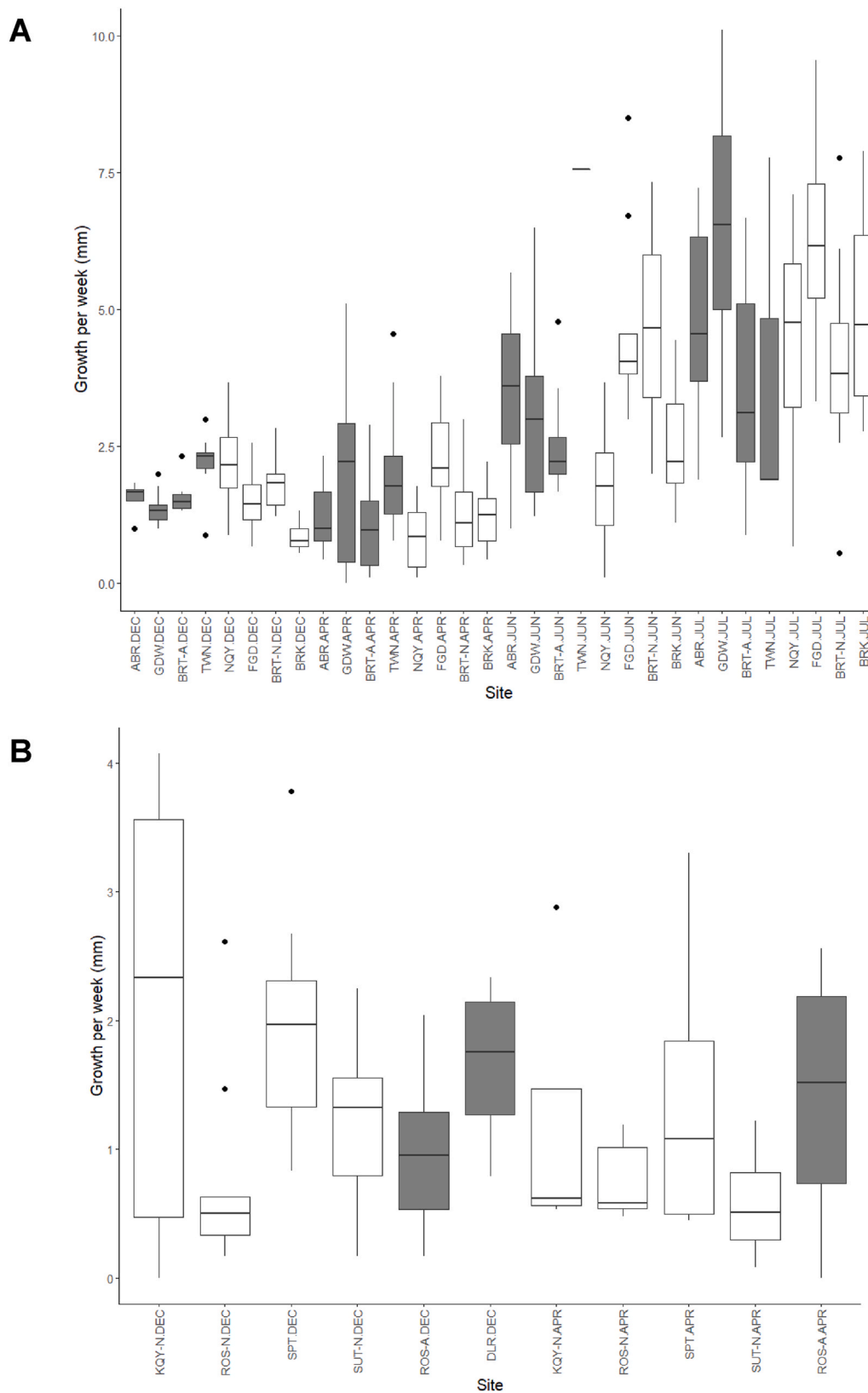


Fig. 3. Growth per week (mm) of *F. vesiculosus* at A) Welsh sites and B) Irish sites. Data for artificial sites in grey, natural sites in white. Note that different scales are used in A and B.

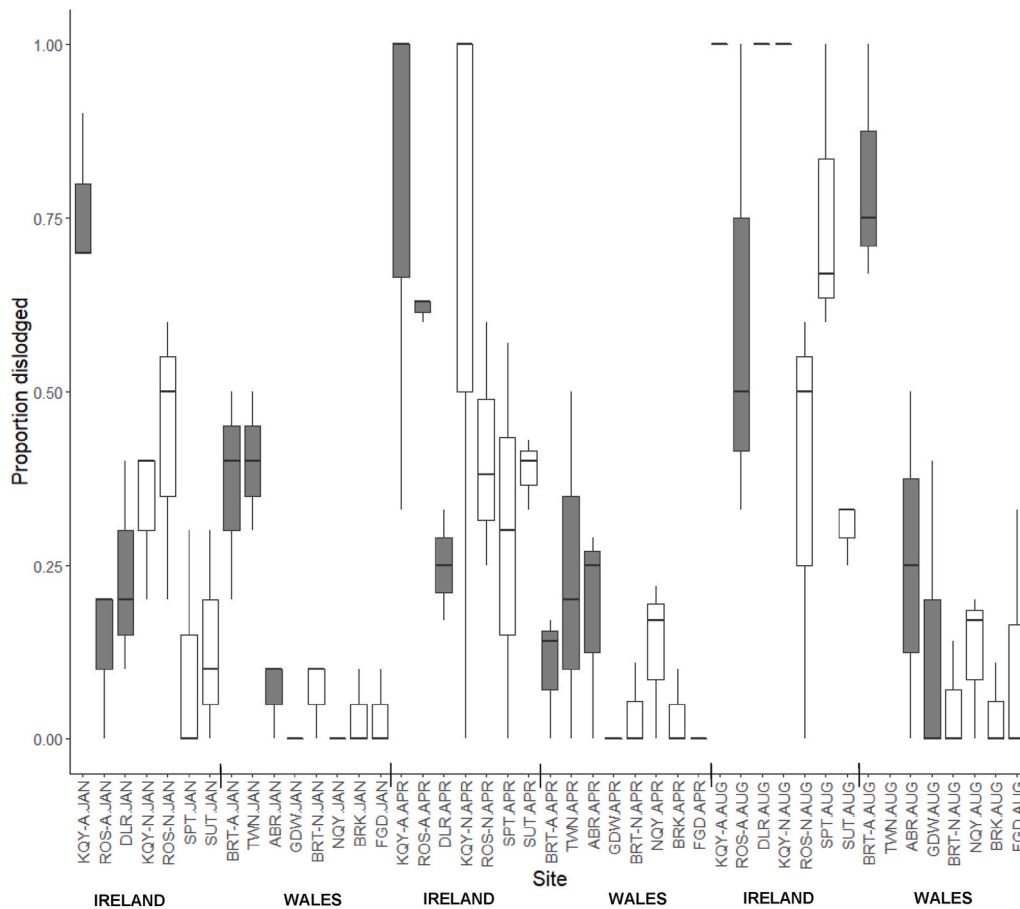


Fig. 4. Proportion of *F. vesiculosus* individuals dislodged in January, April, and August for each site. Data for artificial sites in grey, natural sites in white. No data available for sites TWN, KQY-A, and KQY-N in August.

Table 5

Permutational ANOVAs for dislodgement of *F. vesiculosus* populations between natural rocky reefs and artificial structures along Irish Sea coastlines. Similarity matrix is based on Euclidean distance of the untransformed data. Significance was accepted at $p < 0.05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < 0.01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

| Source of variation | df | F | p |
|-------------------------|-----|-------|---------------|
| Coast = C | 1 | 29.70 | 0.0004 |
| Month = M | 2 | 3.99 | 0.03 |
| Shore Type = T | 1 | 7.97 | 0.02 |
| Site (C x T) = S(C x T) | 11 | 3.04 | 0.001 |
| C x M | 2 | 1.34 | 0.28 |
| C x T | 1 | 0.05 | 0.81 |
| M x T | 2 | 0.70 | 0.51 |
| C x M x T | 2 | 0.07 | 0.94 |
| M x S(C x T) | 22 | 2.79 | 0.0009 |
| Res | 90 | | |
| Total | 134 | | |

slightly greater proportion of ‘fertile’ receptacles was recorded from natural shores than artificial shores (Fig. 8). Furthermore, while artificial shores had a greater proportion of ‘initiated’ receptacles relative to ‘emptying’ receptacles, natural shores showed the opposite pattern (Fig. 8).

4. Discussion

Our results found no differences between artificial structures and natural shores in terms of percentage cover, biomass, or density of *F. vesiculosus*. In general, artificial structures have been found to support a distinct biological assemblage, characterised by lower abundances and fewer species than found on natural shores (Bulleri and Chapman, 2004; Bulleri, 2005b; Bulleri et al., 2005). However, Bulleri and Chapman (2004) demonstrated that the abundance of main-space occupiers does not differ between breakwaters and rocky shores. The artificial sites studied in this investigation comprised largely rip-rap structures, and therefore we postulate that in cases where *F. vesiculosus* is a main-space occupier on an artificial structure, particularly a rip-rap structure, its abundance is comparable to that of populations on natural shores. Rip-rap structures may be made of natural materials and may also have a slope more comparable to that of a natural shore. A high degree of inter-site variability was observed, indicating that percentage cover, biomass, and density are greatly influenced by local environmental variation or differences in the supply of propagules.

Similarly, no differences were observed between artificial structures and natural shores in terms of the growth rate of *F. vesiculosus*. In Wales, where growth rates were monitored throughout the year, growth was similar to that as described in the literature for this species, with a peak during the summer period (Kesar and Larson, 1984; Carlson, 1991).

Differences were, however, observed in terms of dislodgement rates between artificial structures and natural shores, as dislodgement was observed to be higher on artificial structures across all months. A possible explanation for these patterns could be that, in general, marine artificial structures tend to be subject to high levels of both natural and

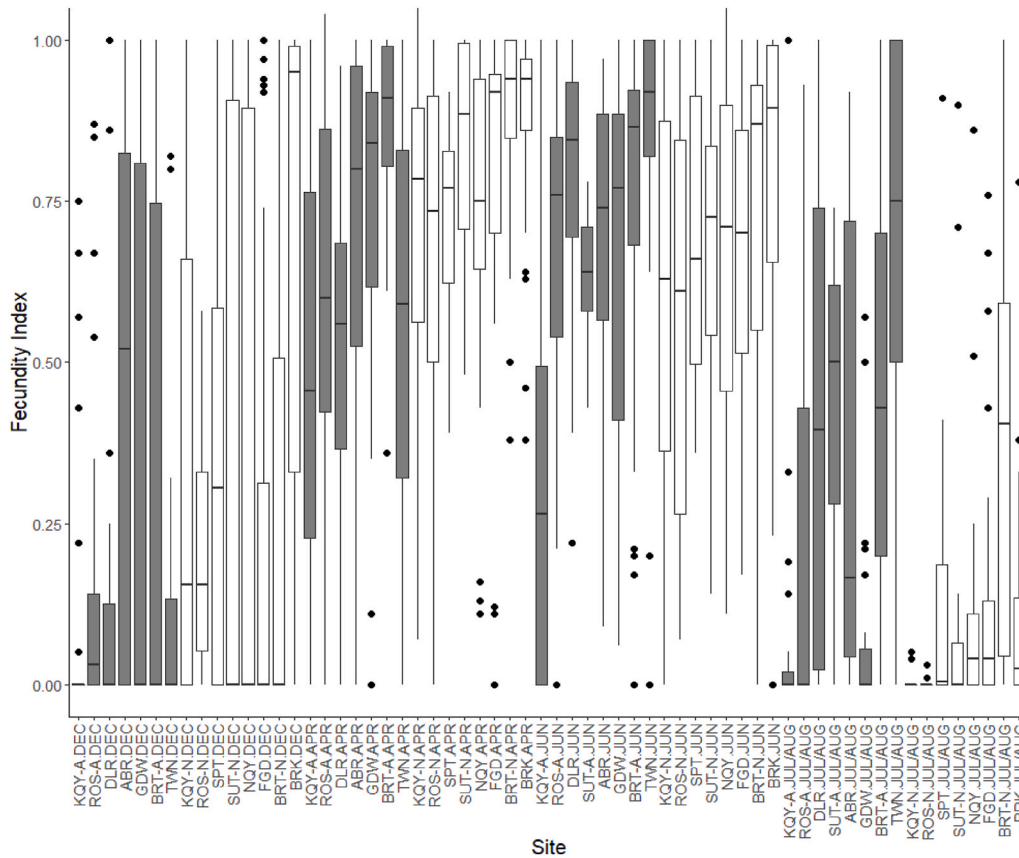


Fig. 5. Fecundity Index of *F. vesiculosus* populations at artificial and natural sites in December, April, June, and July/August. Data for artificial sites in grey, natural sites in white. No data available for SUT-A in December and April.

Table 6

Permutational ANOVAs for Fecundity Index of *F. vesiculosus* populations between natural rocky reefs and artificial structures along Irish Sea coastlines. Similarity matrix is based on Euclidean distance of the untransformed data. Significance was accepted at $p < 0.05$ except when PERMDISP detected significant differences in within-group dispersion between levels of this particular factor, in which case a more conservative p-value was adopted ($p < 0.01$). Underlined p-values indicate where main factors returned significant differences in within-treatment dispersion.

| Source of variation | df | F | p |
|-------------------------|------|-------|---------------|
| Coast = C | 1 | 6.74 | 0.02 |
| Month = M | 4 | 46.76 | 0.0001 |
| Shore Type = T | 1 | 1.21 | 0.28 |
| Site (C x T) = S(C x T) | 12 | 7.73 | 0.0001 |
| C x M | 2 | 0.11 | 0.89 |
| C x T | 1 | 0.51 | 0.50 |
| M x T | 4 | 54.71 | 0.004 |
| C x M x T | 2 | 0.19 | 0.84 |
| M x S(x T) | 34 | 4.95 | 0.0001 |
| Res | 1828 | | |
| Total | 1889 | | |

anthropogenic disturbance, both of which contribute to the loss of individuals and populations (Airoldi and Bulleri, 2011). Consequently, these structures generally support seaweed assemblages consisting of prostrate and encrusting forms, as erect seaweeds are more easily dislodged by wave action (Chapman and Bulleri, 2003). It must also be noted that significant site-level variation in rate of dislodgement from month to month was observed, suggesting that local environmental conditions play an important role in influencing the long-term sustainability of *F. vesiculosus* populations on specific artificial structures.

In addition to the differences in the rate of dislodgement, one of the

Table 7

Analysis of deviance for binomial GLM of *F. vesiculosus* sex ratio between natural rocky reefs and artificial structures along Irish Sea coastlines. Analysis is based on Type III sum of squares. Bold text indicates significance at $p < 0.05$.

| Source of deviance | df | χ^2 | p |
|--------------------|--------|----------|--------------|
| Coast = C | 1 | 0.78 | 0.38 |
| Month = M | 2 | 11.44 | 0.003 |
| Shore Type = T | 1 | 0.15 | 0.70 |
| C x M | 2 | 4.97 | 0.08 |
| C x T | 1 | 4.34 | 0.04 |
| M x T | 2 | 5.02 | 0.08 |
| C x M x T | 2 | 1.72 | 0.42 |
| Res | 85.89 | | |
| Null | 161.04 | | |

most striking differences between the natural shores and artificial structures in this investigation was in terms of reproductive investment. Reproduction in this species follows a seasonal cycle that has been well-documented in the literature (Carlson, 1991; Bäck et al., 1993; Graiff et al., 2017). The populations observed over the course of this investigation displayed the same reproductive cycle as that described in the literature for Atlantic Ocean populations of *F. vesiculosus*: receptacles initiated in December, with maximum production of receptacles occurring in late spring/early summer, with individuals continuing to produce gametes at reduced levels until mid-autumn (Knight and Parke, 1950; Bäck et al., 1993). However, the fecundity index was significantly higher on natural shores during peak reproduction. Furthermore, the fecundity index on natural shores was significantly different between months with a peak in fecundity index in April followed by significant drops in this index in June and July/August. In contrast, the fecundity index on artificial structures remained similar between April and June

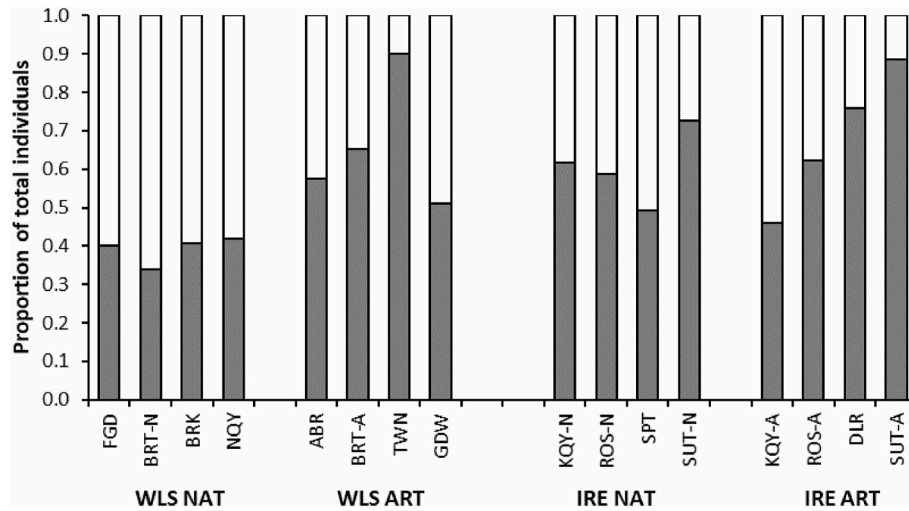


Fig. 6. Proportion of male (white) and female (grey) individuals of *F. vesiculosus* recorded across all months in sites in Ireland (n = 8 sites) and Wales (n = 8 sites).

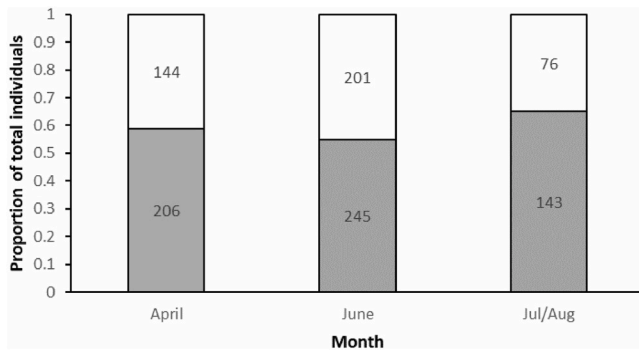


Fig. 7. Proportion of male (white) and female (grey) individuals of *F. vesiculosus* recorded during each month across all of the sites sampled in Ireland (n = 8 sites) and Wales (n = 8 sites). Each column labelled with total individuals in that category.

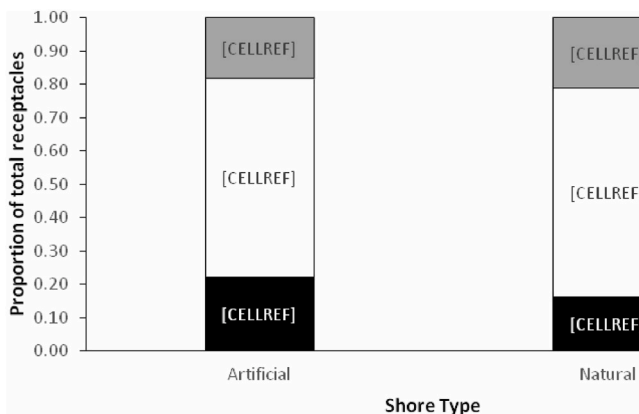


Fig. 8. Proportion of receptacles of each maturity group ('initiated' in black, 'fertile' in white, 'emptying' in grey) recorded from a total of 2107 individuals on artificial (n = 8 sites) and natural shores (n = 8 sites). Each column labelled with total receptacles in that category.

and was higher than the fecundity index on natural shores in July/August. This may suggest a flatter, more elongated reproductive period for *F. vesiculosus* on artificial structures, however study over a greater temporal scale would be required to confirm this pattern. This phenomenon may be related to receptacle development and allocation of

biomass towards reproductive effort. Most *Fucus* species, including *F. vesiculosus*, have a lifespan of 2–3 years and may produce fertile receptacles after their first year (Viana et al., 2015). However, the proportion of reproductive apices produced is much greater after 2 years (Knight and Parke, 1950). We postulate here that the higher rate of loss observed on artificial structures means that fewer individuals reach their second year of life meaning overall allocation of resources towards production of reproductive apices on artificial structures is lower.

While both dislodgement and production of reproductive apices differed significantly between artificial and natural shores, it is important to note that our analyses revealed significant site-level variation for both factors. This small-scale variability suggests that any given artificial structure may support populations of *F. vesiculosus* with dislodgement and production of reproductive apices comparable to that of a natural shore, and therefore it is necessary to consider evidence on a case-by-case basis. Overall, however, there is a tendency for dislodgement to be higher and for production of reproductive apices to be reduced on artificial structures.

Furthermore, in this study we found that a greater proportion of 'initiated' receptacles was recorded overall from artificial structures, while a greater proportion of 'emptying' receptacles was recorded overall from natural shores. This may suggest that the greater number of receptacles produced by individuals on natural shores persist long enough to release gametes into the environment. Further explanations for the patterns found in the current study may be linked to the fact that increased levels of herbivory and physical damage may inhibit reproductive development by forcing fucoid individuals to allocate resources towards the formation of adventitious branches to heal wounds (Kinnby et al., 2019) and by the physical loss of reproductive apices. As artificial structures generally constitute a more high-stress environment than natural shores, these factors may be contributing to decreased production of reproductive apices in *F. vesiculosus* populations highlighted here. All the shores included in this study were characterised by similar levels of wave exposure, therefore it is likely that the main source of disturbance for these populations was driven by sand scouring.

The proportions of male and female individuals appeared to be dependent upon shore type to some extent, with males being more abundant on Welsh natural shores and females being more abundant on Welsh artificial shores. This was not the case for Irish shores where females were more numerous in general. Although the basis for sex determination in *F. vesiculosus* is currently unknown, more recent studies have suggested that a strong genetic component may be at play, possibly involving a male heterogametic (XY) sex chromosome system (Billard et al., 2005; Coelho et al., 2019). Relatively few studies have considered sex ratios of fucoid species in the field. That said it has been postulated

that deviations from a 1:1 male to female ratio may occur at the margins of a species range or in otherwise stressful environments due to differential mortality between sexes (Luthringer et al., 2014). In cases where this results in a female bias, it has been suggested that marginal populations or populations in otherwise stressful environments may be undergoing predominantly asexual reproduction by adventitious branching (Tatarenkov et al., 2005). It is not clear why the sex ratio became increasingly female-biased as the reproductive season progressed. In this study, Irish shores showed higher rates of dislodgement than Welsh shores and artificial structures showed higher rates of dislodgement than natural shores. This may indicate comparatively increased levels of disturbance on Irish shores and artificial structures respectively, resulting in the observed pattern of female bias. There appears to be no record in the literature of situations where differing environmental conditions result in opposite male and female biases, and therefore the male bias on Welsh natural shores observed in this study remains unexplained and would be worth further investigation.

In conclusion, *F. vesiculosus* populations on artificial structures and natural shores appear to differ in terms of their reproductive output, with populations on artificial structures producing fewer 'fertile' receptacles and fewer receptacles overall than those on natural shores. This may be a result of increased rates of dislodgement on artificial structures, leading to populations dominated by individuals in their first year of life. There were no differences in percentage cover, biomass, or density of individuals, and therefore it is possible that *F. vesiculosus* establishes sink populations on artificial structures, with a net absorption of propagules, whereas natural shores constitute source populations, with a net outflow of propagules. This has implications for policy and planning. For example, it may be advisable to consider seeding or transplant techniques to encourage furoid development in cases where artificial structures are constructed at a distance from suitable source populations. This would have wider benefits for the biotic assemblage as a whole, given the characteristics of furoid species as ecosystem engineers. Future investigations should consider looking into whether or not *F. vesiculosus* populations have the ability to support similar associated assemblages on artificial structures and natural shores. More studies like this are needed to help understand the range of impacts of artificial structures on the biology and ecology of marine organisms. Such knowledge and an understanding of the mechanisms leading to any observations of differences between artificial structure and natural shores can help inform eco-engineering solutions, which aim to make artificial structures better for nature.

CRedit author statement

Veronica Farrugia Drakard: Conceptualization, Methodology, Investigation, Formal Analysis, Visualization, Writing – Original Draft.

Paul Brooks: Conceptualization, Methodology, Supervision, Writing – Review & Editing.

Tasman P. Crowe: Conceptualization, Methodology, Supervision, Writing – Review & Editing, Funding Acquisition.

Hannah S. Earp: Methodology, Investigation, Writing – Review & Editing.

Bryan Thompson: Investigation.

Nathan Bourke: Investigation.

Ruby George: Investigation.

Chloe Piper: Investigation.

Pippa J. Moore: Conceptualization, Methodology, Supervision, Writing – Review & Editing, Funding Acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Aguilera, M.A., 2018. Artificial defences in coastal marine ecosystems in Chile: opportunities for spatial planning to mitigate habitat loss and alteration of the marine community structure. *Ecol. Eng.* 120, 601–610. <https://doi.org/10.1016/j.ecoleng.2017.04.021>.
- Airolidi, L., Bulleri, F., 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *PLoS One* 6 (8), e22985. <https://doi.org/10.1371/journal.pone.0022985>.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E Ltd, Devon, United Kingdom.
- Billard, E., Serrão, E.A., Pearson, G.A., Engel, C.R., Destombe, C., Valero, M., 2005. Analysis of sexual phenotype and prezygotic fertility in natural populations of *Fucus spiralis* (Fucaceae, Phaeophyceae) and their putative hybrids. *Eur. J. Phycol.* 40 (4), 397–407. <https://doi.org/10.1080/09670260500334354>.
- Brook, T.W., Gilby, B., Olds, A., Connolly, R.M., Henderson, C., Schlacher, T., 2018. The effects of shoreline armoring on estuarine fish are contingent upon the broader urbanisation context. *Mar. Ecol. Prog. Ser.* 605 <https://doi.org/10.3354/meps12756>.
- Browne, M.A., Chapman, M.G., 2011. Ecologically informed engineering reduces loss of intertidal biodiversity on artificial shorelines. *Environ. Sci. Technol.* 45 (19), 8204–8207. <https://doi.org/10.1021/es201924b>.
- Browne, M.A., Chapman, M.G., 2014. Mitigating against the loss of species by adding artificial intertidal pools to existing seawalls. *Mar. Ecol. Prog. Ser.* 497 <https://doi.org/10.3354/meps10596>.
- Bulleri, F., 2005a. Experimental evaluation of early patterns of colonisation of space on rocky shores and seawalls. *Mar. Environ. Res.* 60 (3), 355–374. <https://doi.org/10.1016/j.marenvres.2004.12.002>, 2005.
- Bulleri, F., 2005b. Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. *Mar. Ecol. Prog. Ser.* 287, 53–65. <https://doi.org/10.3354/meps287053>.
- Bulleri, F., Chapman, M.G., 2004. Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. *Mar. Biol.* 145 (2), 381–391. <https://doi.org/10.1007/s00227-004-1316-8>.
- Bulleri, F., Chapman, M.G., Underwood, A.J., 2005. Intertidal assemblages on seawalls and vertical rocky shores in Sydney Harbour, Australia. *Austral Ecol.* 30 (6), 655–667. <https://doi.org/10.1111/j.1442-9993.2005.01507.x>.
- Bäck, S., Collins, J.C., Russell, G., 1993. Comparative reproductive biology of the Gulf of Finland and the Irish sea *Fucus vesiculosus* L. *Sarsia* 78 (3–4), 265–272. <https://doi.org/10.1080/00364827.1993.10413540>.
- Cacabelos, E., Martins, G.M., Thompson, R., Prestes, A.C.L., Azevedo, J.M.N., Neto, A.I., 2016. Factors limiting the establishment of canopy-forming algae on artificial structures. *Estuar. Coast Shelf Sci.* 181, 277–283.
- Carlson, L., 1991. Seasonal variation in growth, reproduction and nitrogen content of *Fucus vesiculosus* L. In: *The Öresund, Southern Sweden*, vol. 34. Botanica Marina, p. 447.
- Chapman, M.G., Bulleri, F., 2003. Intertidal seawalls—new features of landscape in intertidal environments. *Landsc. Urban Plann.* 62 (3), 159–172. [https://doi.org/10.1016/S0169-2046\(02\)00148-2](https://doi.org/10.1016/S0169-2046(02)00148-2).
- Christie, H., Norderhaug, K., Fredriksen, S., 2009. Macrophytes as habitat for fauna. *Mar. Ecol. Prog. Ser.* 396, 231–243. <https://doi.org/10.3354/meps08351>.
- Clarke, K.R., Gorley, R.N., 2015. Primer V7: User Manual/Tutorial. PRIMER-E Ltd, Devon, United Kingdom.
- Coelho, S.M., Mignerot, L., Cock, J.M., 2019. Origin and evolution of sex-determination systems in the brown algae. *New Phytol.* 222, 1751–1756. <https://doi.org/10.1111/nph.15694>.
- Coombes, M.A., La Marca, E.C., Naylor, L.A., Thompson, R.C., 2015. Getting into the groove: opportunities to enhance the ecological value of hard coastal infrastructure using fine-scale surface textures. *Ecol. Eng.* 77, 314–323. <https://doi.org/10.1016/j.ecoleng.2015.01.032>.
- Dayton, P.K., 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Systemat.* 16, 215–245.
- Dennis, H.D., Evans, A.J., Banner, A.J., Moore, P.J., 2018. Reefcrete: reducing the environmental footprint of concretes for eco-engineering marine structures. *Ecol. Eng.* 120, 668–678. <https://doi.org/10.1016/j.ecoleng.2017.05.031>.

- Dethier, M., et al., 1993. Visual versus random-point percent cover estimations: "objective" is not always better. *Mar. Ecol. Prog. Ser.* 96, 93. <https://doi.org/10.3354/meps096093>.
- Evans, A.J., Firth, L.B., Hawkins, S.J., Morris, E.S., Goudge, H., Moore, P.J., 2015. Drill-cored rock pools: an effective method of ecological enhancement on artificial structures. *Mar. Freshw. Res.* 67 (1), 123–130.
- Fauvelot, C., Bertozzi, F., Costantini, F., Airolidi, L., Abbiati, M., 2009. Lower genetic diversity in the limpet *Patella caerulea* on urban coastal structures compared to natural rocky habitats. *Mar. Biol.* 156, 2313–2323. <https://doi.org/10.1007/s00227-009-1259-1>.
- Ferrario, F., Ivesa, L., Jaklin, A., Perkol-Finkel, S., Airolidi, L., 2016. The overlooked role of biotic factors in controlling the ecological performance of artificial marine habitats. *J. Appl. Ecol.* 53 (1), 16–24. <https://doi.org/10.1111/1365-2664.12533>.
- Firth, L., Browne, K., Knights, A., Hawkins, S., Nash, R., 2016. Eco-engineered rock pools: a concrete solution to biodiversity loss and urban sprawl in the marine environment. *Environ. Res. Lett.* 11, 094015 <https://doi.org/10.1088/1748-9326/11/9/094015>.
- Firth, L., Mieszkowska, N., Thompson, R., Hawkins, S., 2013. Climate change and adaptational impacts in coastal systems: the case of sea defences. *Environ. Sci. Process. Impact* 15. <https://doi.org/10.1039/c3em00313b>.
- Firth, L.B., Schofield, M., White, F.J., Skov, M.W., Hawkins, S.J., 2014a. Biodiversity in intertidal rock pools: informing engineering criteria for artificial habitat enhancement in the built environment. *Mar. Environ. Res.* 102, 122–130. <https://doi.org/10.1016/j.marenvres.2014.03.016>.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airolidi, L., Bouma, T.J., Hawkins, S.J., 2014b. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. *Coast Eng.* 87, 122–135. <https://doi.org/10.1016/j.coastaleng.2013.10.015>.
- Graiff, A., Dankworth, M., Wahl, M., Karsten, U., Bartsch, I., 2017. Seasonal variations of *Fucus vesiculosus* fertility under ocean acidification and warming in the western Baltic Sea. *Bot. Mar.* 60 <https://doi.org/10.1515/bot-2016-0081>.
- Green, D.S., Chapman, M.G., Blockley, D.J., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecol. Eng.* 46, 1–10. <https://doi.org/10.1016/j.ecoleng.2012.04.030>.
- Hurd, C.L., Harrison, P.J., Bischof, K., Lobban, C.S., 2014. *Seaweed Ecology and Physiology*. Cambridge University Press.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Keser, M., Larson, B.R., 1984. Colonization and growth dynamics of three species of *Fucus*. *Mar. Ecol. Prog. Ser.* 15 (1), 125–134.
- Kinnby, A., Pereyra, R.T., Havenhand, J.N., De Wit, P., Jonsson, P.R., Pavia, H., Johannesson, K., 2019. Factors affecting formation of adventitious branches in the seaweeds *Fucus vesiculosus* and *F. radicans*. *BMC Ecol.* 19 (1), 22. <https://doi.org/10.1186/s12898-019-0239-7>.
- Knight, M., Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *F. serratus* L. *J. Mar. Biol. Assoc. U. K.* 29 (2), 439–514. <https://doi.org/10.1017/S0025315400055454>.
- Lenth, R., 2020. Emmeans: estimated marginal means, aka least-squares means. R package version 1.5.1. <https://CRAN.R-project.org/package=emmeans>.
- Luthringer, R., Cormier, A., Ahmed, S., Peters, A.F., Cock, J.M., Coelho, S.M., 2014. Sexual dimorphism in the brown algae. *Perspect. Phycol.* 1 (1), 11–25.
- Mayer-Pinto, M., Dafforn, K.A., Bugnot, A.B., Glasby, T.M., Johnston, E.L., 2018. Artificial structures alter kelp functioning across an urbanised estuary. *Mar. Environ. Res.* 139, 136–143. <https://doi.org/10.1016/j.marenvres.2018.05.004>.
- Mayer-Pinto, M., Dafforn, K.A., Johnston, E.L., 2019. A decision framework for coastal infrastructure to optimize biotic resistance and resilience in a changing climate. *Bioscience* 69 (10), 833–843. <https://doi.org/10.1093/biosci/biz092>.
- Mayer-Pinto, M., Ledet, J., Crowe, T. P., & Johnston, E. L. (in press). Sublethal effects of contaminants on habitat forming species may affect marine ecosystem functioning: a review and meta-analysis of corals, seaweeds, saltmarsh, seagrass and shellfish. *Biol. Rev.*
- Moreira, J., Chapman, M.G., Underwood, A.J., 2006. Seawalls do not sustain viable populations of limpets. *Mar. Ecol. Prog. Ser.* 322, 179–188.
- Morris, R.L., Chapman, M.G., Firth, L.B., Coleman, R.A., 2017. Increasing habitat complexity on seawalls: investigating large- and small-scale effects on fish assemblages. *Ecol. Evol.* 7, 9567–9579. <https://doi.org/10.1002/ece3.3475>.
- Moschella, P.S., Abbiati, M., Åberg, P., Airolidi, L., Anderson, J.M., Bacchiocchi, F., et al., 2005. Low-crested coastal defence structures as artificial habitats for marine life: using ecological criteria in design. *Coast Eng.* 52, 1053–1071.
- Naylor, L.A., Coombes, M.A., Venn, O., Roast, S.D., Thompson, R.C., 2012. Facilitating ecological enhancement of coastal infrastructure: the role of policy, people and planning. *Environ. Sci. Pol.* 22, 36–46. <https://doi.org/10.1016/j.envsci.2012.05.002>.
- Parke, M., 1948. Studies on British Laminariaceae. I. Growth in *Laminaria Saccharina* (L.) Lamour. *J. Mar. Biol. Assoc. U. K.* 27 (3), 651–709. <https://doi.org/10.1017/S0025315400056071>.
- Piñeiro-Corbeira, C., Barreiro, R., Cremades, J., Arenas, F., 2018. Seaweed assemblages under a climate change scenario: functional responses to temperature of eight intertidal seaweeds match recent abundance shifts. *Sci. Rep.* 8 (1), 12978. <https://doi.org/10.1038/s41598-018-31357-x>.
- Rinne, H., Salovius-Laurén, S., 2020. The status of brown macroalgae *Fucus* spp. and its relation to environmental variation in the Finnish marine area, northern Baltic Sea. *Ambio* 49 (1), 118–129. <https://doi.org/10.1007/s13280-019-01175-0>.
- Rothäusler, E., Rugiu, L., Jormalainen, V., 2018. Forecast climate change conditions sustain growth and physiology but hamper reproduction in range-margin populations of a foundation rockweed species. *Mar. Environ. Res.* 141, 205–213. <https://doi.org/10.1016/j.marenvres.2018.09.014>.
- RStudio, 2019. RStudio: Integrated Development for R. RStudio Inc, Boston, MA. Retrieved from. <http://www.rstudio.com/>.
- Ruuskanen, A., Bäck, S., 1999. Does environmental stress affect fertility and frond regeneration of *Fucus vesiculosus*? *Ann. Bot. Fenn.* 36 (4), 285–290.
- Tatarenkov, A., Bergström, L., Jönsson, R.B., Serrão, E.A., Kautsky, L., Johannesson, K., 2005. Intriguing asexual life in marginal populations of the brown seaweed *Fucus vesiculosus*. *Mol. Ecol.* 14, 647–651.
- Teagle, H., Hawkins, S.J., Moore, P.J., Smale, D.A., 2017. The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J. Exp. Mar. Biol. Ecol.* 492, 81–98. <https://doi.org/10.1016/j.jembe.2017.01.017>.
- Vadas, R.L., Steneck, R.S., 1988. Zonation of deep water benthic algae in the Gulf of Maine. *J. Phycol.* 24, 338–346.
- Vadas, R.L., Wright, W.A., Beal, B.F., 2004a. Biomass and productivity of intertidal rockweeds (*Ascophyllum nodosum* LeJolis) in Cobscook Bay. *Northeast. Nat.* 11 (2), 123–142.
- Vadas, R.L., Beal, B.F., Wright, W.A., Steve, N., Sheri, E., 2004b. Growth and productivity of sublittoral fringe kelps (*Laminaria longicruris*) Bach. Pyl. in Cobscook Bay, Maine. *Northeast. Nat.* 11, 143–162.
- Viana, I.G., Bode, A., Fernández, C., 2015. Ecology of *Fucus vesiculosus* (Phaeophyceae) at its southern distributional limit: growth and production of early developmental stages. *Eur. J. Phycol.* 50 (3), 247–259. <https://doi.org/10.1080/09670262.2015.1013159>.